TEMPERATURE ADAPTATIONS OF COPEPOD EGGS FROM THE ARCTIC TO THE TROPICS

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The purpose of this paper is not simply to show once again that temperature adaptation occurs in physiological processes of poikilotherms from different latitudes. It also demonstrates what appears to be the simplest way of expressing such adaptation by a single parameter, and suggests that the relationship between this parameter and environmental temperature may be sufficiently close to allow prediction of development rate of copepod eggs from different latitudes.

Use is made of an expression developed by Bělehrádek (1935) relating physiological rates and temperatures:

$$V = a (T - \alpha)^b$$

where V is the observed rate, T is the temperature, and a, b and α are fitted constants. Other three-constant equations may be equally accurate, but, as has been shown elsewhere (McLaren, 1963), this equation reveals differences between rate-temperature curves in the simplest and most direct way. Each constant defines a unique property of such curves: a describes differences in slope, b is adequate to account for differences in monotonic curvilinearity within *natural* temperature ranges and α ("biological zero") may be well below the natural temperature range, but defines positions of curves on the (arbitrary) Celsius scale.

It has long been known that large eggs tend to develop more slowly than small eggs among related organisms (Berrill, 1935). For different races of the frog *Rana pipiens* in the United States, choice of a single estimate of b for all races reveals a simple proportionality between egg diameter and a of Bělehrádek's equation (McLaren, 1965). The same is true among different populations of the same species or among closely related species of copepods (McLaren, 1966). Another equation, actually isomorphic with Bělehrádek's with b taken as -1.0, has been used to describe development time of nematode eggs (Crofton and Whitlock, 1965); the β of their equation, equivalent to a in Bělehrádek's, was shown to be close related to egg volume. There is, therefore, empirical justification for assuming that a single value of b applies among related species, since doing so reveals a simple relationship between egg size and development rate.

If b is the same among related species, and a is a constant of proportionality, then α remains as the "real" indicator of temperature adaptation. A previous

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TABLE I

*Development times to hatching of copepod eggs at different temperatures.   Each experiment is a
single egg sac carried by a female, or a batch of eggs produced more-or-less synchronously
by one or more females*

Species	Locality	Number of experiments	Mean temperature (°C)	Days to hatching	
				Mean	Range
Pseudocalanus minutus	Halifax	17	0	10.70	10.07–11.14
		11	2.73	6.92	7.71– 7.16
		4	5.35	5.06	4.90– 5.31
		11	9.27	3.48	3.38– 3.58
		8	11.43	3.06	2.79– 3.56
		14	12.01	2.90	2.75– 3.00
Acartia clausi	Halifax	2	0	15.58	15.33–15.84
		3	4.88	5.98	5.88– 6.05
		3	10.80	2.78	2.69– 2.87
Tortanus discaudatus	Halifax	1	0	19.71	
		3	4.85	8.15	8.00– 8.25
		3	10.80	3.93	3.82– 3.98
Calanus glacialis	Frobisher, N.W.T.	1	0	6.35	
		1	2.60	4.30	
		1	5.23	3.23	
		1	7.92	2.61	
Calanus hyperboreas	Halifax	3	0	6.67	6.50– 6.75
		2	3.34	4.30	4.23– 4.38
		4	6.89	2.98	2.90– 3.02
Metridia longa	Halifax	2	0	4.20	
		2	3.08	2.93	2.88– 2.98
		1	3.53	2.76	
		2	7.69	1.73	
		1	11.96	1.34	
Temora longicornis	Halifax	2	0	10.81	10.79–10.84
		3	3.26	6.47	6.35– 6.55
		3	7.39	3.71	3.52– 3.83
		6	11.83	2.32	2.27– 2.38
Eurytemora hirundoides	Halifax	1	0	13.27	
		2	3.17	7.80	7.74– 7.85
		1	11.80	2.82	
Centropages furcatus	Jamaica	1	15.85	2.83	
		3	17.60	2.00	1.96– 2.08
		3	20.21	1.17	1.08– 1.27
		3	25.78	0.74	0.66– 0.86
		3	29.43	0.58	0.50– 0.66
Acartia tonsa	Narragansett Bay	1	10.0	6.0	
		38	11–12	4.75	4.17– 5.33
		6	14–15	3.0	2.80– 3.20
		5	15.4–16.2	2.3	2.01– 2.59
		5	24.5–26.1	0.68	0.66– 0.70
Calanus finmarchicus	Tromso, Norway	6	0		4.83– 5.41
		12	5		2.46– 2.71
		9	13–14		0.96– 1.08
		3	20		0.83– 1.00

study (McLaren, 1966), largely concerned with the effects of egg size and yolk concentration on the value of a, revealed only slight differences in α for egg development among several geographically distant populations of the copepod *Pseudocalanus minutus*.   However, α was 3–4° C lower for three species whose ranges extend to arctic waters than for two temperate species.   The present paper extends the analysis to several more species, and attempts a more direct determination of the relationship between α and environmental temperature.

Materials and Methods

Experimental methods have been described elsewhere (McLaren, 1966). Briefly, each experiment on Table I involved a single egg sac carried by a female or a group of free eggs produced more-or-less synchronously by one or more females, and kept at controlled temperatures until all viable eggs hatched.   Experimental salinities were not always determined, but the influence of salinity on development rate is probably negligible within natural ranges (McLaren, Walker, and Corkett, 1968).

Results

Development times (with fiducial limits) of the first four species on Table I have been published previously (McLaren, 1966), but additional experiments have been added for two of these..   Data for *Calanus finmarchicus* are from Marshall and

1. *Metridia longa*, $a = 1099$, $\alpha = -15.1$
2. *Calanus finmarchicus*, $a = 1122$, $\alpha = -14.1$
3. *Calanus glacialis*, $a = 1491$, $\alpha = -14.5$
4. *Calanus hyperboreas*, $a = 1555$, $\alpha = -14.3$
5. *Pseudocalanus minutus*, $a = 2144$, $\alpha = -13.4$
6. *Temora longicornis*, $a = 1346$, $\alpha = -10.4$
7. *Eurytemora hurundoides*, $a = 1640$, $\alpha = -10.4$
8. *Acartia clausi*, $a = 1163$, $\alpha = -8.2$
9. *Tortanus discaudatus*, $a = 1785$, $\alpha = -9.0$
10. *Acartia tonsa*, $a = 489$, $\alpha = 1.8$
11. *Centropages furcatus*, $a = 422$, $\alpha = 3.7$

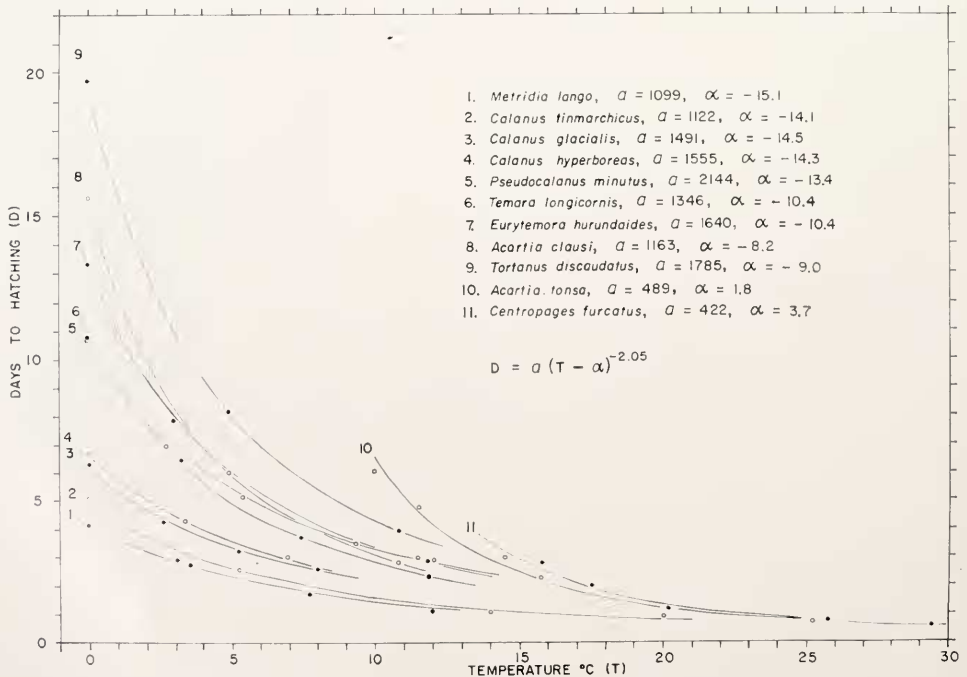$$D = a (T - \alpha)^{-2.05}$$

FIGURE 1.   Bělehrádek's temperature functions fitted to mean or median times to hatching of copepod eggs (data on Table I).

Orr (1953). Resting eggs were reported earlier in *Acartia tonsa* (Zillioux, 1969) and some eggs in this study also showed dormancy at 14–15° C and below. The values on Table I are, however, for normal, uninterrupted development.

Bĕlehrádek's temperature functions were fitted to determine the best single estimate of b for all species on Table I except *Acartia tonsa* and *Calanus finmarchicus,* for which temperatures and times are available only as ranges in some instances. This was done by successive approximation by computer to the value of b (nearest 0.05) giving the smallest sum of standard errors of the regressions for all points for each species: log (development time) $=$ log $a + b$ log $(- \alpha)$. This value of $b = -2.05$ was then used to estimate a and α from unweighted median times and temperatures for *A. tonsa* and *C. finmarchicus* as well.
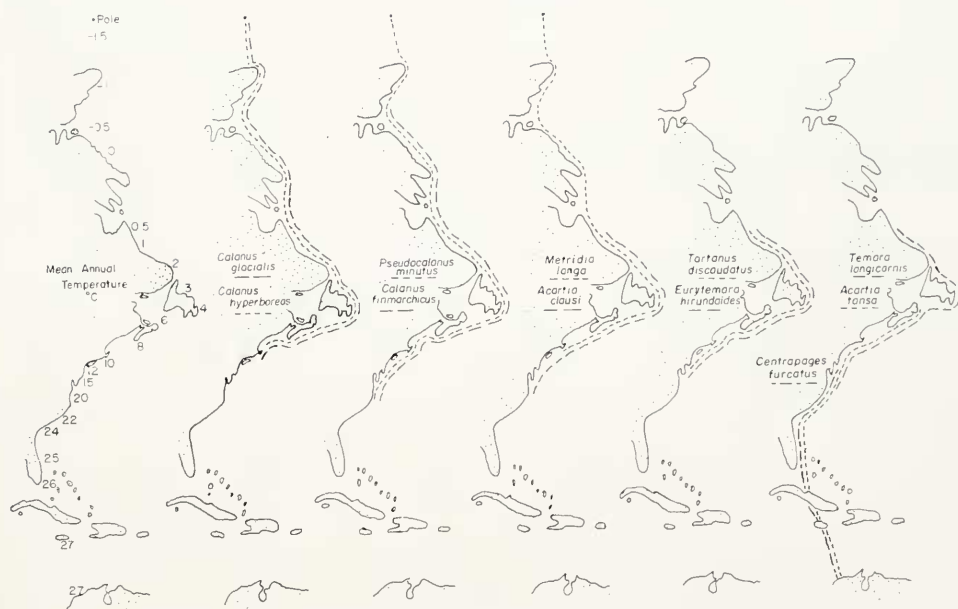
FIGURE 2. Mean annual temperatures and distributions of copepods between the North Pole and South America.

The resulting curves, transformed to a linear plot, are shown with their respective constants on Figure 1. Clearly the curves fit the various data well (the correlation coefficients of the logarithmic regressions exceed 0.99 for all species except *Centropages furcatus* at 0.98). The deviations of points for *A. tonsa* may be attributed to use of medians for times and temperatures (*cf.* Table 1).

A proportionate relationship between a (Fig. 1) and egg diameter is confirmed for the three species of *Calanus.* Eggs of C. finmarchicus are about 145 μ in diameter (Marshall and Orr, 1953), those of *C. glacialis* are about 179 μ (McLaren, 1966) and a single measured egg of *C. hyperboreas* was 190 μ. However, an earlier conclusion (McLaren, 1966) based on limited data, that greater yolkiness of eggs would slow down their development rate and therefore increase a, is not

born out. Eggs of *C. hyperboreas* are much more opaque, apparently because large amounts of yolk stored for non-feeding young stages (Conover, 1967), than are eggs of *C. glacialis* (McLaren, 1966), but *a* values of these species seem to be explicable in terms of egg size alone.

The values of α on Figure 1 show a logical relationship with environment; northern forms have low values and warm-water species have high values of α. Much information on geographical distributions of the species on the east coast of the United States is summarized by Deevey (1960) and Wilson (1932). Northern limits can be established for northern Labrador (Carter, 1965), Ungava Bay (Fontaine, 1955) and the high arctic of Canada and the Arctic Ocean (Grainger,
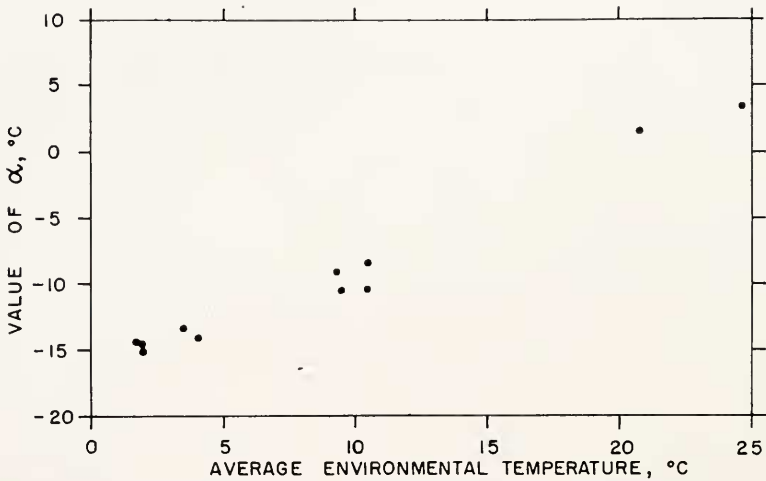

FIGURE 3. Relationship between α ("biological zero") of Bĕlehrádek's temperature function for eggs of eleven species of copepods and estimates of average temperature in their environmental ranges.

1965). Range maps are available for the three species of *Calanus* in North America (Grainger, 1963). *Eurytemora hirundoides* is recorded from as far south as Chesapeake Bay (Wilson, 1932) and as far north as Northern Labrador (Carter, 1965); some or all records may be referred to *E. affinis* (Deevey, 1960), but this probably does not affect the results in this paper. Distributions of each species on Table 1 between the North Pole and South America are summarized on Figure 2. The animals may, of course, be seasonal or local within these ranges, and doubtless successful breeding is geographically more restricted.

Among geographically widely separate populations of *Pseudocalanus minutus* and *Calanus finmarchicus*, α varied less than 1° C (McLaren, 1966). This suggests that α is genetically adapted to conditions of the species' whole geographical range (and allows the use of α as determined from experiments on *Calanus finmarchicus* from Norway to approximate the value of α for the same species in North America). There is no precise way to determine the average temperatures to which a species may be subjected, but a crude approximation has been attempted by using mean annual surface temperatures calculated from mean monthly surface temperatures

(Meteorological Office, London, 1948; U. S. Navy Hydrographic Office, 1957) along the latitudinal ranges of the species (Fig. 2). The resulting relationship between α and "average environmental temperature" is shown on Figure 3.

DISCUSSION

We conclude that a single parameter of temperature response (α) can be used to describe differences in temperature adaptation of development rate of eggs of related species. The relationship between α and approximate environmental temperature is so close that it may be possible to predict development rate at any temperature of eggs of copepods of known geographical range from experiments at a single temperature. It should be understood that these approaches do not depend on any theoretical assumptions. The mathematical resolution of such three-constant functions is rather low so that purely empirical curves, in which all constants are fitted, may show wide variations in the values of b. Assuming that b has the same value for all species may have no biological basis, and may not even be correct within specified limits of accuracy. The justifications for this assumption are the statistical adequacy of the resulting curves (Fig. 1), the aforementioned relationship between egg size and a, and the equally striking relationship between α and evironmental temperature that is revealed in this paper. Clearly these relationships are of some interest.

The results may also be compared with certain traditional approaches to temperature adaptation. The approach seems much simpler than attempting to quantify relationships between environmental temperature and differences in "Q_{10}," shifts in weight-metabolism curves, "rotation" or "translation" of semi-logarithmic plots, and other similar modes of expression (examples in Rose, 1967). A recent analysis of temperature adaptation of amphibian embryos by Bachman (1969), who does not refer to an earlier analysis of some of the same material (McLaren, 1966), assumes that the relationship between temperature and development rate is linear within the temperature range that permits high survival of embryos. This is equivalent to using Bělehrádek's equation with $b = 1.0$, and leads to values of "$T_o + 10$" ($= \alpha + 10$) as a measure of temperature adaptation. (In using development time at $T_o + 10$ as another measure of temperature adaptation, Bachman fails to note the independent effects of egg size described earlier by McLaren.) Determining $T_o + 10$ from a linear regression may be arithmetically simpler, but cannot be generally accurate; development rate of copepod eggs, for example, is more nearly a square function ($b = 2$) than a linear function of temperature.

Although the usefulness of Bělehrádek's function does not depend on theoretical assumptions, it is tempting to attach some biological meaning to its constants. The ways by which egg size might affect the value of a have been discussed in previous papers (McLaren, 1965, 1966). Although differences in a may in some sense be involved in temperature adaptation—since rates will be speeded up or slowed down at any temperature—it seems intuitively satisfying to think of true temperature adaptation simply as a shift of the entire curve on the temperature scale as expressed through changes in α. Whether the underlying mechanisms involve changes in biophysical restrictions on biochemical rates (Bělehrádek, 1935; McLaren, 1965, 1966) or are explicable by more sophisticated

reaction-rate theories (*e.g.*, Hochachka and Somero, 1968) it can be argued that molecular explanations of adaptation in development rate of copepod and other eggs should account for the rather simple relationship between α and environmental temperature.

Summary

The development times to hatching (D) of eggs of eleven species of copepods are closely described as functions of temperature (T) by Bĕlehrádek's temperature function, $D = a (T - \alpha)^b$ using the assumption that the same value of b applies to all species. The value of a is related to egg diameter among three species of *Calanus*, and is unaffected by the greater opacity (presumably yolkiness) of eggs of *C. hyperboreas*. The value of α remains as the "real" indicator of temperature adaptation, and is closely and linearly related to estimates of environmental temperature based on mean annual temperatures within the range of each species between the pole and South America, along the east coast of the Americas.

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